E-Article

Propensity for Risk in Reproductive Strategy Affects Susceptibility to Anthropogenic Disturbance

Enrico Pirotta,[1,2,*] Vincent Hin,[3] Marc Mangel,[4,5] Leslie New,[1] Daniel P. Costa,[5,6] André M. de Roos,[3] and John Harwood[7]

1. Department of Mathematics and Statistics, Washington State University, Vancouver, Washington 98686; 2. School of Biological, Earth, and Environmental Sciences, University College Cork, Cork T23 N73K, Ireland; 3. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, The Netherlands; 4. Theoretical Ecology Group, Department of Biology, University of Bergen, Bergen 9020, Norway; 5. Institute of Marine Sciences, University of California, Santa Cruz, California 95064; 6. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060; 7. Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews KY16 9LZ, United Kingdom

Submitted October 29, 2019; Accepted April 14, 2020; Electronically published August 31, 2020

Online enhancements: appendixes, code.

ABSTRACT: Animals initiate, interrupt, or invest resources in reproduction in light of their physiology and the environment. The energetic risks entailed in an individual's reproductive strategy can influence the ability to cope with additional stressors, such as anthropogenic climate change and disturbance. To explore the trade-offs between internal state, external resource availability, and reproduction, we applied state-dependent life-history theory (SDLHT) to a dynamic energy budget (DEB) model for long-finned pilot whales (*Globicephala melas*). We investigated the reproductive strategies emerging from the interplay between fitness maximization and propensity to take energetic risks, as well as the resulting susceptibility of individual vital rates to disturbance. Without disturbance, facultative reproductive behavior from SDLHT and fixed rules in the DEB model led to comparable individual fitness. However, under disturbance, the reproductive strategies emerging from SDLHT increased vulnerability to energetic risks, resulting in lower fitness than fixed rules. These fragile strategies might therefore be unlikely to evolve in the first place. Heterogeneous resource availability favored more cautious (and thus more robust) strategies, particularly when knowledge of resource variation was accurate. Our results demonstrate that the assumptions regarding the dynamic trade-offs underlying an individual's decision-making can have important consequences for predicting the effects of anthropogenic stressors on wildlife populations.

* Corresponding author; email: enrico.pirotta@wsu.edu.

ORCIDs: Pirotta, https://orcid.org/0000-0003-3541-3676; Hin, https://orcid.org/0000-0002-9497-1224; Mangel, https://orcid.org/0000-0002-9406-697X; Costa, http://orcid.org/0000-0002-0233-5782; de Roos, https://orcid.org/0000-0002-6944-2048.

Am. Nat. 2020. Vol. 196, pp. E71–E87.
DOI: 10.1086/710150

Keywords: dynamic energy budget, resource availability, life-history trade-offs, marine mammals, population consequences of disturbance, stochastic dynamic programming.

Introduction

Over the course of their lives, animals make decisions (i.e., choose a behavior from a suite of options) in light of their current physiological state, their experiences, and the state of the environment (Stearns 1992). Decisions such as when to reproduce, when to abandon an ongoing reproductive attempt, or how much energy to transfer to offspring are central to an individual's fitness and emerge from the trade-off between the cost of current investments and future reproductive potential (Hirshfield and Tinkle 1975). This trade-off is particularly relevant for long-lived species, which often have the option to delay or abandon reproduction and compensate later, when conditions are more advantageous (Eberhardt 2002). The reproductive strategies resulting from these decisions can lead to inter-individual variation in the age at first reproduction, the interval between reproductive attempts, and the pattern of parental care. This variation will entail varying levels of risk among individuals, where risk is defined as the potential for a reduction in individual vital rates that results from behavior leading to a poor energetic state.

Within its physiological constraints, an animal in optimal body condition is more risk tolerant, because energy reserves provide a buffer against variability in energy intake from food resources (Zera and Harshman 2002). Moreover, the propensity for risky behavior is predicted to vary over time because of changes in the reproductive potential of

the individual and variation in resource availability (Frank and Slatkin 1990; Roff 1993). In environments with high resource availability that does not vary or varies in ways that individuals can anticipate (i.e., predictably), animals can take more risks associated with reproduction, because the reliability of resources means that they can cover unanticipated costs. In contrast, unpredictable fluctuations in resource availability over time may lead to a more cautious strategy—where an individual avoids situations that could endanger its survival—and to greater behavioral plasticity (Snell-Rood 2013). Thus, the intensity and predictability of resource variation will determine the optimal reproductive strategy (Dall and Johnstone 2002).

Life-history traits influence the susceptibility of a population to new stressors in the environment (Stark et al. 2004; Sibly et al. 2013), such as climate change or disturbance resulting from human activities. Aside from purely physiological responses (e.g., increased stress levels) and acute repercussions on individual vital rates (e.g., injury or death), the effect of disturbance-inducing stressors will be mediated by a disrupted energy balance via the interruption of foraging activity or the costs of avoidance, which will affect the ability to invest in growth, survival, and reproduction (Pirotta et al. 2018*a*, 2019). When resource availability is heterogeneous, the consequences of anthropogenic disturbance could be severe if the disturbance coincides with periods of low resource availability (Costa 2012; Hin et al. 2019). In a predictable environment, disturbance may also have an impact on individual vital rates if reproductive decisions have evolved to favor energetic risks and lack of plasticity (Meyers and Bull 2002; Hendry 2016). In these ways, disturbance could lead to markedly different outcomes depending on the reproductive strategy and associated propensity to take energetic risks.

Assessments of the population-level effects of disturbance from human-related stressors are required under many regulatory frameworks (e.g., European Habitats Directive 92/43/EEC; US Marine Mammal Protection Act, 16 US Code § 1361 et seq.; and Endangered Species Act, 16 US Code § 1531 et seq.). However, quantifying the long-term effects of physiological and behavioral changes is challenging (Gill et al. 2001; National Academies 2017). To bridge the gap between observable responses and management requirements, the population consequences of disturbance (PCoD) framework formalizes the functional steps linking short- and long-term population-level effects (Pirotta et al. 2018*a*). While originally developed for disturbances affecting marine mammals, the PCoD framework has broad applications in both marine and terrestrial systems. The links between behavioral changes and individual physiological state, which influence individual vital rates and are required by the PCoD framework, are in most contexts difficult to empirically quantify. However, bioenergetic models of an individual's energy uptake and allocation have been successfully used to inform these links (Farmer et al. 2018; McHuron et al. 2018; Pirotta et al. 2018*a*, 2018*b*, 2019; Hin et al. 2019). The dynamic energy budget (DEB) model framework used by Hin et al. (2019) provides an example that relies on simple decision rules that are fixed functions only of the internal state of the animal and are hence not derived from fitness optimization in specific environments (Kooijman 2009). Once a DEB model is developed, disturbance can be simulated as an additional component, offering a tool for managers to assess proposed activities before consent. However, assumptions on the rules of energy allocation, particularly around the interplay between maximizing reproductive output and minimizing energetic risk, could have a strong influence on emerging behavioral and reproductive patterns and thus on the predicted effects of simulated disturbance.

In contrast to the fixed rules underpinning DEB models, state-dependent life-history theory (SDLHT) uses stochastic dynamic programming (SDP) to identify behavioral and reproductive strategies that maximize a given fitness criterion. Strategies in SDP are summarized as a matrix of decisions that maximize expected lifetime reproductive output (our adopted fitness measure) as a function of time and internal and external state (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). Therefore, this approach explicitly explores the multidimensional space in which animals make decisions. Derived, optimized behaviors can then be used in simulations to predict an individual's fitness without and with exposure to additional disturbance sources (McHuron et al. 2017, 2018; Pirotta et al. 2018*b*, 2019). These models can also be used to investigate how various sources of uncertainty—both in resource availability and in an individual's knowledge of the system—affect decisions and the resulting life-history strategies. More generally, this framework addresses the question of the propensity for risk-taking and how it varies depending on the physiology of an organism and available resources.

In this study, we use SDLHT to explore the role of propensity for risk-taking and its interplay with fitness on an individual's reproductive strategy. Specifically, we reformulate an existing DEB model for a long-lived marine mammal species—the long-finned pilot whale *Globicephala melas* (Hin et al. 2019)—using SDP and compare how life-history strategies derived from fixed and fitness-maximization rules affect an individual's susceptibility to disturbance. We then explore the role of physiological constraints to reproductive investments, heterogeneous resource availability, and individual knowledge of the environment on the propensity for risk-taking and the predicted effects of disturbance. We also show how SDP models can be used to quantify the

sensitivity of predictions from DEB models with respect to their fixed underlying rules.

Methods

Dynamic Energy Budget Model

Hin et al. (2019) developed a bioenergetic model for the acquisition and use of energy of a female medium-sized cetacean, which they parametrized using data on long-finned pilot whales. Their model was built on the DEB model developed by de Roos et al. (2009) and describes energy acquisition from feeding (and, for a calf, suckling) and female energy allocation to metabolism, growth in body size, pregnancy, and lactation. Energy acquisition from feeding depends on the density of resources on a given day of the year, t, $R(t) = \bar{R} \cdot [1 + A \cdot \sin(2\pi t/365)]$, where $\bar{R}$ represents the mean resource density and A represents the relative amplitude of seasonal resource variation. Available energy is stored in a reserve compartment, mainly composed of fat stored in adipose tissue. Body condition, as indicated by the size of these reserves relative to total body mass, affects an individual's ability to survive and reproduce and is thus an important indicator of health. An individual's target body condition, ρ (defined as the body condition at which feeding effort is 50% of the maximum rate), is assumed to be constant and equal to 0.3. The authors also define a starvation threshold $\rho_s = 0.15$, below which an individual experiences starvation-induced mortality.

Hin et al. (2019) use a series of rules to determine when a female initiates reproduction and how much energy she invests in her calf. These rules are fixed, in the sense that they are defined a priori and depend only on female internal state (i.e., her body condition). Briefly, a female is assumed to initiate a reproductive cycle whenever her reserve mass exceeds a threshold that corresponds to the energy required to offset starvation and the costs of fetal growth and development. Once a cycle is initiated, abortion is not possible, even if the female's state changes drastically. However, after the calf is born and the female is lactating, she regulates milk provisioning in response to her body condition, given the requirements of the calf (fig. 1). These requirements depend on body condition and age of the calf. Relative milk provisioning from the mother declines with decreasing body condition and equals one when her condition is equal to the target ρ and zero when her condition falls below the starvation threshold ρ_s (fig. 1*C*). Consequently, the female may entirely cease to provide milk before the end of the lactation period (for more details, see Hin et al. 2019 and app. A; apps. A–G are available online).

Hin et al. (2019) used the model to predict the consequences of anthropogenic disturbance—simulated as a period of no feeding activity of variable duration (5–50 days) recurring every year—on life expectancy, lifetime reproductive output, age at first reproduction, age at first weaning, and interbirth interval. Survival is determined by two processes: age-related mortality and starvation-induced mortality; however, only starvation-induced mortality was considered when assessing the consequences of disturbance across the entire lifetime of a female. Age-related mortality was used to calculate expected lifetime reproductive output, which represents the joint outcome of survival and reproduction.

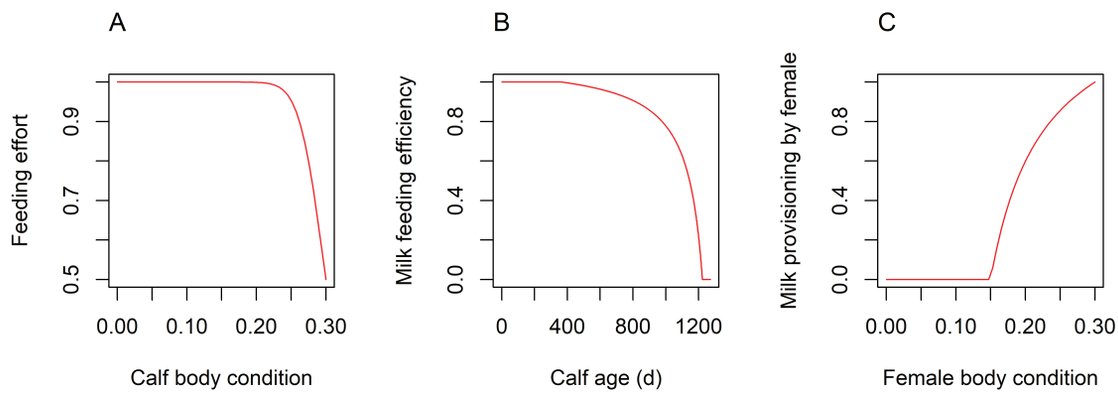

Figure 1: Rules determining the amount of milk delivered by the female during lactation in Hin et al. (2019), assuming target body condition $\rho = 0.3$ and starvation threshold $\rho_s = 0.15$. *A*, Feeding effort of the calf as a function of its body condition. *B*, Milk feeding efficiency, declining over the course of lactation (i.e., for increasing calf age). *C*, Milk provisioning as a function of female body condition; this last component was modified to a binary decision in the stochastic dynamic programming model.

Stochastic Dynamic Programming Adaptation

Building on the underlying DEB model of Hin et al. (2019), we used SDLHT (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000) to allow three decisions to be facultative: (1) initiating a new reproductive cycle, (2) interrupting an ongoing pregnancy (i.e., aborting the fetus), and (3) delivering the milk required by the calf on a given day (as in fig. 1*A*, 1*B*), thus replacing the relationship with female body condition in figure 1*C*. SDHLT requires the definition of a set of physiological state variables (here, given female age: female body condition and, when applicable, waiting stage, fetus age, calf age, and calf body condition; see below) that vary in response to individual reproductive behavior and external resource availability, as well as a measure of Darwinian fitness (here, female lifetime reproductive output; see below). At every age a (in days) of the female, we used SDLHT to identify the optimal reproductive decision—that is, the decision that maximized expected lifetime reproductive output from age a onward given the current values of the state variables. The expectation was taken over stochastic events of mortality.

We restricted the option to initiate a reproductive cycle to 12 times per year, thus constraining birth and weaning dates. This simplification allowed us to retain female ability to reproduce throughout the year, while making the model computationally feasible. We take t to indicate the day of the year (DOY, varying between 0 and 364 days). We set $t = 0$ days to the middle of spring (i.e., when resource density is at its mean value and increasing, as in Hin et al. 2019), and hereafter, all relevant dates are presented under the assumption that the simulated female was born (i.e., age $a = 0$ days) on $t = 260$ days and entered the model in the fourth year after birth on $t = 23$ days, as a newly weaned individual aged $a = T_L = 1{,}223$ days. A female pilot whale may live up to 60 years (Hin et al. 2019). We set maximum age to the first possible weaning date ($t = 268$ days; table 1) after reaching 60 years, resulting in a time horizon of $T = 365$ days/year $\cdot$ 60 years + (268 days − 260 days) = 21,908 days.

Reproductive States and State Transitions

Throughout her life, a female can be in one of five reproductive states (McHuron et al. 2018): (1) resting (not waiting, not pregnant, and not lactating), (2) waiting, (3) pregnant, (4) lactating, or (5) lactating and waiting (during the last year of lactation). For a female that has decided to initiate reproduction, the waiting state represents the average time required until the beginning of pregnancy, given ovulation rate and the chance of successful insemination (Hin et al. 2019).

Starting 1 year after the female is weaned (Hin et al. 2019), a resting female can decide to enter the waiting state 12 times per year (on DOY $\mathbf{t_w}$; table 1). She then must wait $T_D = 445$ days before the onset of pregnancy (on DOY $\mathbf{t_p}$; table 1). Unless a female aborts the fetus, the calf is born after $T_P = 365$ days (on DOY $\mathbf{t_b} = \mathbf{t_p}$). After $T_L = 1{,}223$ days, a calf is weaned (on DOY $\mathbf{t_l}$; table 1). In the last 365 days of lactation, a female can decide to enter the waiting state and initiate a new reproductive cycle on DOY $\mathbf{t_w}$.

State Variables and Mortality

We characterize a female of age a by five state variables (table 1), the first being her condition $X(a)$, expressed as the ratio $B(a)/W(a)$, where $B(a)$ represents the mass of fat reserves, $W(a) = B(a) + S(a)$ represents total body mass, and $S(a)$ represents age-dependent structural mass. When a female is pregnant, $W(a) = B(a) + S(a) + S_f(\tau_p)$, where $S_f(\tau_p)$ represents the mass of the fetus given fetal age $\tau_p = T(a)$. The state variable $X(a)$ varies between $x_{\min} = 0$ and $x_{\max} = 0.31$. For computational reasons, we varied female body condition in increments of 0.01. The second state variable is the condition of her calf $X_c(a)$ (when the female is lactating)—that is, the ratio of calf reserve to total body mass $B_c(a)/W_c(a)$. Given the calf's current age $a_c = A_c(a)$, $W_c(a) = B_c(a) + S(a_c)$. For $X_c(a)$, we used the same extremes and increment size as $X(a)$. The third state variable is the number of days in the current waiting state $D(a)$, varying between 0 and $T_D = 445$ days, the duration of the waiting period. The fourth state variable is the number of days in the current pregnant state $T(a)$ (i.e., the age of the fetus), varying between 0 and $T_P = 365$ days, the duration of gestation. The fifth state variable is the number of days in the current lactating state $A_c(a)$ (i.e., the age of the dependent calf), varying between 0 and $T_L = 1{,}223$ days, the duration of lactation. The state variable $X(a)$ applies to all reproductive states, whereas the other state variables apply only to specific reproductive states (for details of the state-dependent dynamics of the state variables, see app. C). We let $M(a)$ represent age-related daily probability of mortality (when applicable) and $M_s(B(a), W(a))$ represent the starvation-induced daily probability of mortality (table 1; for a discussion of the form of these functions, see Hin et al. 2019).

Fitness Function and SDP Equations

A female's fitness is defined as her expected lifetime reproductive output. Lifetime reproductive output increases whenever a calf is successfully raised until weaning ($A_c(a) = T_L$), as defined by the indicator function: $\varphi[A_c(a)] = 1$ if $A_c(a) = T_L$ and 0 otherwise. Details of

Table 1: Overview of main model variables and parameters

Variable, parameter	Description	Value
t	Day of the year (DOY)	0–364 days
$\bar{R}$	Mean resource density	1.8 (in model V1)
A	Amplitude of seasonal resource variation	0, .15, .3, .45
$R(t)$	Resource density on DOY t	$\bar{R} \cdot [1 + A \cdot \sin(2\pi t/365)]$
a	Female age	T_L–T
s	Female reproductive state	1–5
$X(a) = x$	Female body condition	$x_{\min}$–$x_{\max}$
$X_c(a) = x_c$	Calf body condition	$x_{\min}$–$x_{\max}$
$D(a) = d$	No. days in current waiting state	0–T_D
$T(a) = \tau_p$	No. days in current pregnant state	0–T_P
$A_c(a) = a_c$	No. days in current lactating state	0–T_L
$x_{\min}$	Minimum body condition	0
$x_{\max}$	Maximum body condition	.31
x_{c0}	Calf condition at birth	.15
$X(T_L)$	Female initial condition	.264
ρ	Target body condition	.3
ρ_s	Starvation threshold	.15
T	Time horizon (maximum age)	21,908 days
T_D	Duration of waiting period	445 days
T_P	Duration of gestation	365 days
T_L	Duration of lactation	1,223 days
$\mathbf{t_w}$	DOY on which a female can initiate waiting	0, 30, 60, 90, 120, 150, 180, 210, 240, 270, 300, 330 days
$\mathbf{t_p}$	DOY on which a female can implant	15, 45, 80, 110, 140, 170, 200, 230, 260, 290, 320, 350 days
$\mathbf{t_b}$	DOY on which a female can give birth	15, 45, 80, 110, 140, 170, 200, 230, 260, 290, 320, 350 days
$\mathbf{t_l}$	DOY on which a female can wean her calf	23, 53, 83, 113, 143, 173, 208, 238, 268, 298, 328, 358 days
$B(a)$	Mass of fat reserves	See Hin et al. 2019
$S(a)$	Structural mass	See Hin et al. 2019
$S_f[T(a)]$	Fetus mass	See Hin et al. 2019
$W(a)$	Total body mass	$B(a) + S(a) + S_f[T(a)]$ when pregnant, $B(a) + S(a)$ otherwise
$B_c(a)$	Calf reserve mass	See Hin et al. 2019
$W_c(a)$	Calf total body mass	$B_c(a) + \mathrm{S}[A_c(a)]$
$\varphi[A_c(a)]$	Increment in lifetime reproductive output	1 if $A_c(a) = T_L$, and 0 otherwise
$F_s(x, \ldots, a)$	Maximum expected accumulated lifetime reproductive output for a female of age a in state s	See appendix B (available online)
$M(a)$	Age-related mortality	$\alpha_1 \cdot e^{-\beta 1 \cdot a} + \alpha_2 \cdot e^{-\beta 2 \cdot a}$, where $\alpha_1 = 4.01\mathrm{e}{-4}$, $\alpha_2 = 6.04\mathrm{e}{-6}$, $\beta_1 = 5.82\mathrm{e}{-4}$, and $\beta_2 = 3.01\mathrm{e}{-4}$ (for details, see Hin et al. 2019)
$M_s(B(a), W(a))$	Starvation-induced mortality	$\mu_s \cdot [\rho_s \cdot W(a)/B(a) - 1]_+$, where $\mu_s = .2$ (for details, see Hin et al. 2019)

Note: The irregular spacing of $\mathbf{t_p}$, $\mathbf{t_b}$, and $\mathbf{t_l}$ is caused by the year lasting 365 days and the last interval among $\mathbf{t_w}$ thus being 5 days longer than all others.

the SDP equations are reported in appendix B. We solved SDP equations backward in time, starting from the last day of a female's life ($a = T$), using Rcpp (Eddelbuettel and Francois 2011) for R (R Core Team 2019). Doing so generated the matrices of optimal time- and state-dependent decisions that maximized future female lifetime reproductive output for every combination of her state variables at age a.

Simulated Scenarios

We used the matrices of optimal reproductive decisions obtained from SDP in Monte Carlo simulations (forward iteration) to model the state dynamics, survival, and lifetime reproductive output of 1,000 females from weaning until death. We replicated the environmental and anthropogenic disturbance scenarios in Hin et al. (2019; table A1;

tables A1, E1, and F1 are available online). Simulated disturbance represents worst-case, extreme scenarios that were used for demonstration. We followed Hin et al. (2019) and set female initial condition $X(T_L) = 0.264$. The Rcpp code for the backward and forward iterations of the model is available in a zip file as well as in the Open Science Framework repository: https://osf.io/g8dq2 (Pirotta et al. 2020).[1]

Fitness Benefit of Alternative Reproductive Decisions

To investigate the processes affecting an individual's decision-making, we defined the fitness benefit of a specific reproductive decision over a particular alternative as the difference between their respective fitness values (see app. D). A negative value indicated a fitness cost. We extracted fitness values from a model with age-related mortality, a mean resource density $\bar{R} = 1.8$, and no seasonality $A = 0$. We also assessed changes in the fitness benefit for varying resource densities ($\bar{R} = 1.6$ and $\bar{R} = 2$, fixing A at 0) and amplitudes of seasonality ($A = 0.15$ and $A = 0.3$, fixing $\bar{R}$ at 1.8).

Model Variants

There may be constraints to the timing and amount of a female's energy investment toward reproduction—for example, a minimum body size before she can reproduce (Martin and Rothery 1993; Sand 1996) or some physiological regulation of the volume or quality of the milk transferred to the calf (Crocker et al. 2001; Chan-McLeod et al. 2009). These constraints will affect the sensitivity and flexibility of her reproductive strategy when experiencing unforeseen food limitation (e.g., as a consequence of disturbance). Moreover, different baseline levels of resource variability will imply different expectations of future resource availability, affecting a female's willingness to take energetic risks, but this will depend on her knowledge of resource availability and distribution in heterogeneous landscapes (Dall and Johnstone 2002). Therefore, we developed a series of variants of the basic model (hereafter, version V1) to investigate the role of different components of female reproduction (version V2), resource availability (versions V3 and V4), and individual knowledge of resource availability (version V4) in determining the emerging reproductive strategy, a female's willingness to take energetic risks, and the consequences for female susceptibility to anthropogenic disturbance (tables 2, F1). In these variants, we excluded the effect of age-related mortality—that is, a female (and her calf) could die only due to starvation—and we assumed that mean resource density was $\bar{R} = 1.8$.

Version V2: Graded Milk Delivery. Rather than limiting milk delivery to the calf to all the milk required or no milk at all, we let a lactating female decide to deliver 0%, 25%, 50%, 75%, or 100% of the milk required each day (model V2.1). As in model V1, the decision on lactation replaced the dependence on female condition in the DEB model (as in fig. 1*C*). This version enabled us to test whether model results were affected by a female's lactation strategy, particularly her ability to fine-tune the amount of milk delivered. As an additional constraint on top of graded milk delivery, we tested the effect of a minimum age at first reproduction (age at first reproduction ≥8.68 years; model V2.2).

Version V3: Daily Resource Variation. We introduced stochastic (uncorrelated) daily variation in resource availability. For simplicity, we restricted this assessment to three potential resource conditions: average, 50% higher than average, and 50% lower than average. On 90% of days, resources were in average condition—that is, the realized density of resources on a given day t of the year $\tilde{R}(t) = R(t)$. For the remaining days, the realized resource density had an equal chance of being either 50% higher (i.e., $\tilde{R}(t) = R(t) \cdot 1.5$) or 50% lower (i.e., $\tilde{R}(t) = R(t) \cdot 0.5$) than the average conditions $R(t)$. In practice, in the backward iteration a female's decision was based on the weighted mean of the fitness values associated with the three resource conditions (average, 50% higher, and 50% lower), given the probabilities of these conditions occurring. In the forward iteration, a multinomial draw determined the resource condition a female encountered on any given day. For simplicity, this variant was tested only under two seasonality scenarios: $A = 0$ and $A = 0.15$.

Version V4: Yearly Resource Variation. We allowed resource availability to vary on a yearly scale: in good years, $\bar{R}_g = \bar{R} \cdot 1.1$, while in bad years, $\bar{R}_b = \bar{R} \cdot 0.9$. There was a 70% probability of resource availability persisting from one year to the next. We varied the level of knowledge of resource availability that a female had. In model V4.1, a female optimized her strategy under the assumption that resources varied on a daily scale; in other words, she accounted for bad resource availability but had no understanding of the temporal scale of the variation or memory of previous conditions. In model V4.2, the female knew that resources varied from year to year and behaved in light of a correct perception of the current condition and the expected transition probabilities between conditions. If a female was disturbed on a given day, she used

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

Table 2: Summary of model variants implemented in the state-dependent life-history theory approach

Model variant	Description	Milk delivery	Resource variability	Amplitude of seasonality
V1	Basic model	Binary (0% or 100% of calf requirements)	No	0, .15, .3, .45
V2	Graded milk delivery	Graded (0%, 25%, 50%, 75%, or 100% of calf requirements)	No	0, .15, .3, .45
V3	Stochastic daily resource variation	Binary (0% or 100% of calf requirements)	Daily, 50%	0, .15
V4	Yearly resource variation	Binary (0% or 100% of calf requirements)	Yearly, perceived as daily (V4.1); yearly, correctly perceived, adjusting reproductive behavior following disturbance (V4.2)	0, .15

the optimal strategy for bad yearly conditions in the following day. For these variants, we tested two seasonality values: $A = 0$ and $A = 0.15$.

Results

Baseline Scenarios without Disturbance

In the absence of disturbance, mean life-history statistics were largely comparable to the ones obtained by Hin et al. (2019), with and without age-related mortality and with varying amplitude in resource seasonality (table E1; cf. figs. 2–4 in Hin et al. 2019). Without age-related mortality, females avoided starvation-induced mortality and survived until the maximum age, with the exception of scenarios with the largest amplitude of seasonal resource variation $A = 0.45$, where many females died at a young age when their maximum reserves could not buffer periods of low resource availability. As in Hin et al. (2019), lifetime reproductive output was dictated by the length of time required for a reproductive cycle, resulting in 11 calves (i.e., 5.5 female calves on average). Lifetime reproductive output decreased at amplitudes of seasonality greater than $A = 0.15$. Overall, females tended to start reproducing earlier than in the DEB model, as reflected in the lower age at first reproduction, but the first attempt was unsuccessful, and thus age at first weaning was higher. This first failed attempt also led to a slightly shorter interbirth interval.

Despite the similarities in realized vital rates, the ability of a female to choose to deliver milk affected the time series of her and the calf's reserve mass (fig. E1 [figs. E1–E10 and F1–F8 are available online]; cf. fig. 2 in Hin et al. 2019). The best strategy for a female in a nonseasonal environment was to deliver milk consistently in the first phase of lactation and then nurse irregularly during the calf's transition to autonomous feeding, trading off her own and the calf's condition (fig. E2). The female interrupted milk delivery earlier than in the DEB model, anticipating the moment she began to rebuild her own reserves and thus extending the time spent in better condition at the expense of the calf. As a result, she was able to achieve a higher peak condition and maintain higher condition when not lactating (fig. E1; cf. fig. 2 in Hin et al. 2019). In a seasonal environment, she alternated periods of milk delivery with periods of no delivery, but she still reduced milk delivery earlier than in the DEB model, as reflected in the time series of her body condition (fig. E3; cf. fig. 3 in Hin et al. 2019). Reserve dynamics were also affected by her inability to modulate the amount of milk delivered, which resulted in her condition declining more rapidly during lactation, reaching a lower trough.

Differences in Fitness between Alternative Reproductive Decisions

On the basis of the fitness benefit (i.e., the difference in future, expected lifetime reproductive output) of entering the waiting state, model V1 predicted that individuals initiated a reproductive cycle whenever possible because waiting had no energetic cost. The exception was a short window of time at a young age when females were too small to sustain the costs of reproduction and attempting to do so caused the loss of a safer opportunity later (fig. 2). After peaking around age 10, the relative advantage of entering the waiting state decreased with age as reproductive potential decreased. The fitness benefit also decreased with body condition for females that were starving (i.e., $X(a) \leq 0.15$). When $X(a) \sim 0.08$ or less, there was no difference in fitness between waiting and resting, because females were unlikely to be able to sustain a complete reproductive cycle (i.e., these attempts would likely be abandoned at the pregnancy stage; see below). These findings

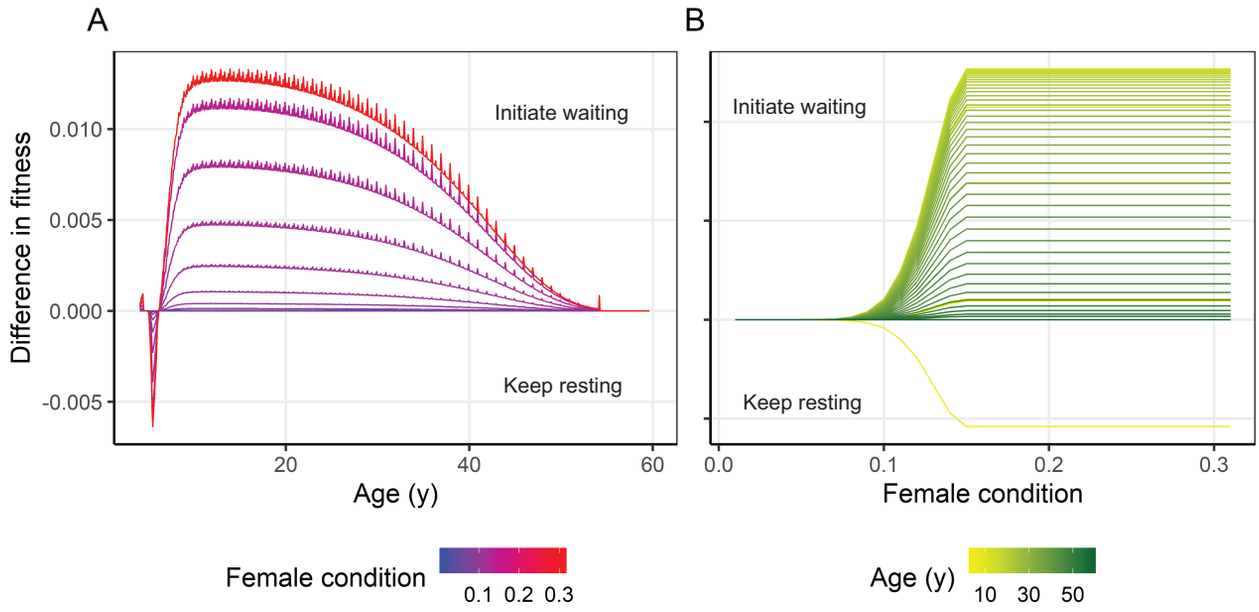

Figure 2: Difference in fitness value in model V1 between the decision to initiate the waiting period and the decision to keep resting, highlighting the costs or benefits of engaging in reproduction as a function of age by condition of the female (*A*) and as a function of condition by age (*B*). Peaks in fitness difference in *A* are due to the restriction on the dates for the initiation of waiting: some dates correspond to a higher benefit because they warrant an extra calf at the end, starting from the last peak corresponding to the last calf that can be raised to weaning.

held true for the decision to start waiting when already lactating: the age and condition of the suckling calf had little to no effect on fitness differences (fig. E5).

Early in gestation, it was generally more advantageous in model V1 to continue the pregnancy even when in poor condition, because of the small associated costs (fig. 3). However, as gestation progressed, aborting could become the better choice if females were in poor condition. In general, fitness differences between choices were stronger in the later stages of gestation, when gestation costs were higher. The advantage of continuing a pregnancy decreased as age increased because of the smaller remaining reproductive potential. The influence of body condition on the decision was also stronger at younger ages, with mostly younger individuals aborting in poor condition. The threshold of condition for continuing a pregnancy to be beneficial over abortion was also higher for younger females. In extremely poor condition, there was no difference in fitness between decisions, because females were unlikely to survive.

Regarding milk delivery, our model predicted that it was advantageous for females to deliver milk when they were not starving ($X(a) > 0.15$) and the calf was in poor (but not very poor) condition ($0.02 < X_c(a) \leq 0.15$; fig. 4). The models predicted that females below the starvation threshold did not deliver milk. For intermediate values of female and calf body condition, there was a switch in optimal decision as age increased (fig. 4), because the same body condition for older females corresponded to a larger absolute reserve mass, and these females could therefore deliver milk at lower relative risk. Similarly, the threshold of condition at which it started to be advantageous to deliver milk decreased with age. As for other reproductive decisions, the decision to deliver milk made no difference for females in very poor condition, because they were unlikely to survive, or for very old females, with little reproductive potential. The decision to deliver milk while both waiting and lactating was influenced by female and calf age and condition in the same way as for females that were only lactating (fig. E6).

Seasonal resources caused oscillations in fitness outcomes for all decision processes over the course of the year. There were periods when it was particularly advantageous to initiate the waiting period; this depended on the alignment of later phases of the reproductive cycle (pregnancy and lactation, which have a substantial energetic cost) with the oscillations of resource availability (e.g., fig. E7). Moreover, there was a tendency to delay the first reproductive attempt, because the associated risk increased with seasonality. The decision to continue a pregnancy was less affected by seasonality, which primarily changed the magnitude of the fitness advantage of continuing

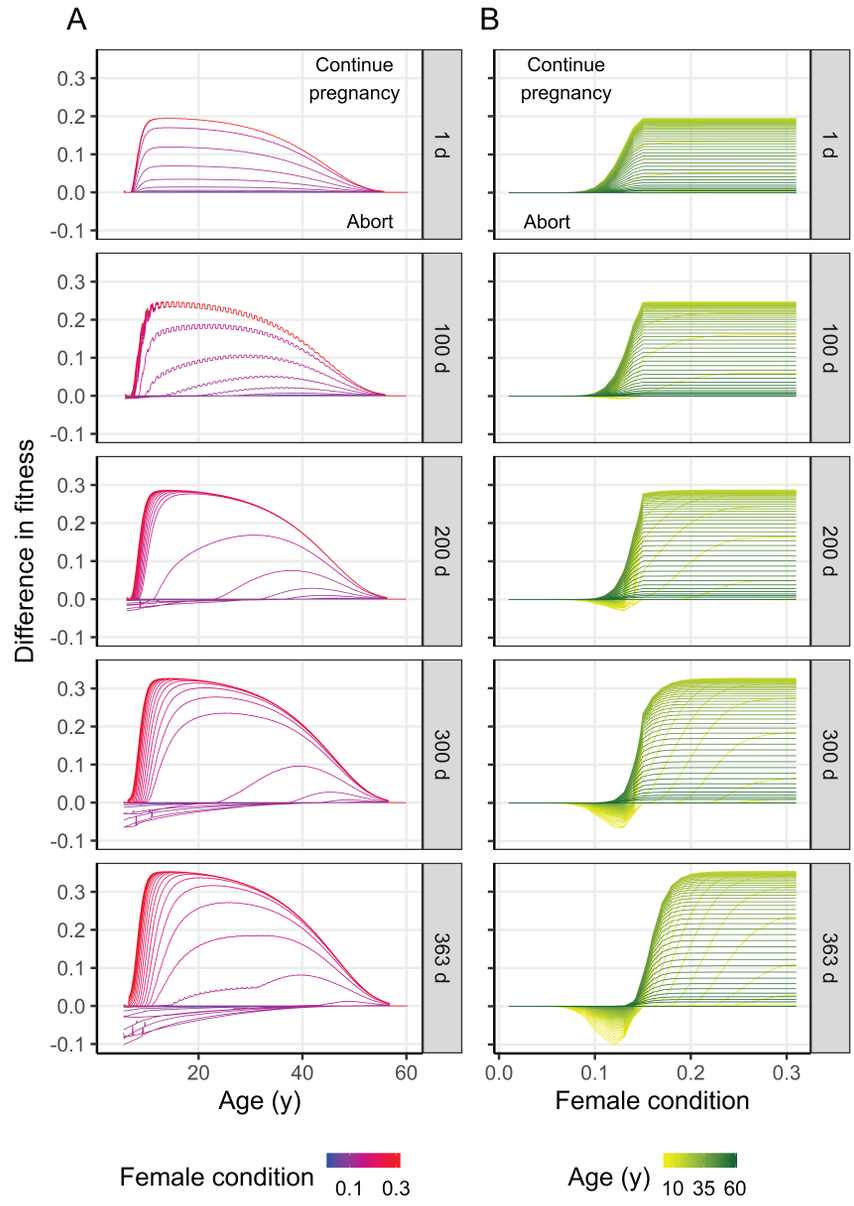

Figure 3: Difference in fitness value in model V1 between the decision to continue a pregnancy and the decision to abort the fetus, highlighting the costs or benefits of continuing pregnancy as a function of age by condition of the female (*A*) and as a function of condition by age (*B*) at five stages of gestation (after 1, 100, 200, 300, or 363 days of gestation). The oscillations in fitness benefits in *A* emerge from the constraints on the timing of reproduction and depend on which timings ensure weaning a calf on the last day of life. For some gestation stages, these oscillations are more apparent because of the relative size of the associated fitness (there is either a greater benefit of continuing pregnancy or a greater cost of interrupting it, depending on the energy that has already been invested).

pregnancy. Finally, seasonal oscillations in fitness differences could result in a shift in the decision to deliver milk at a given time of the year. For example, not delivering milk tended to be preferred in winter—when resource availability was lower—by females in sufficiently good condition (e.g., fig. E8).

When mean resource density was high, the advantage of initiating a reproductive cycle, continuing pregnancy, and delivering milk extended to younger ages and females in comparatively poorer body condition (e.g., fig. E9). In contrast, lower resource availability caused a reduction in the overall fitness benefit of these decisions and a delay

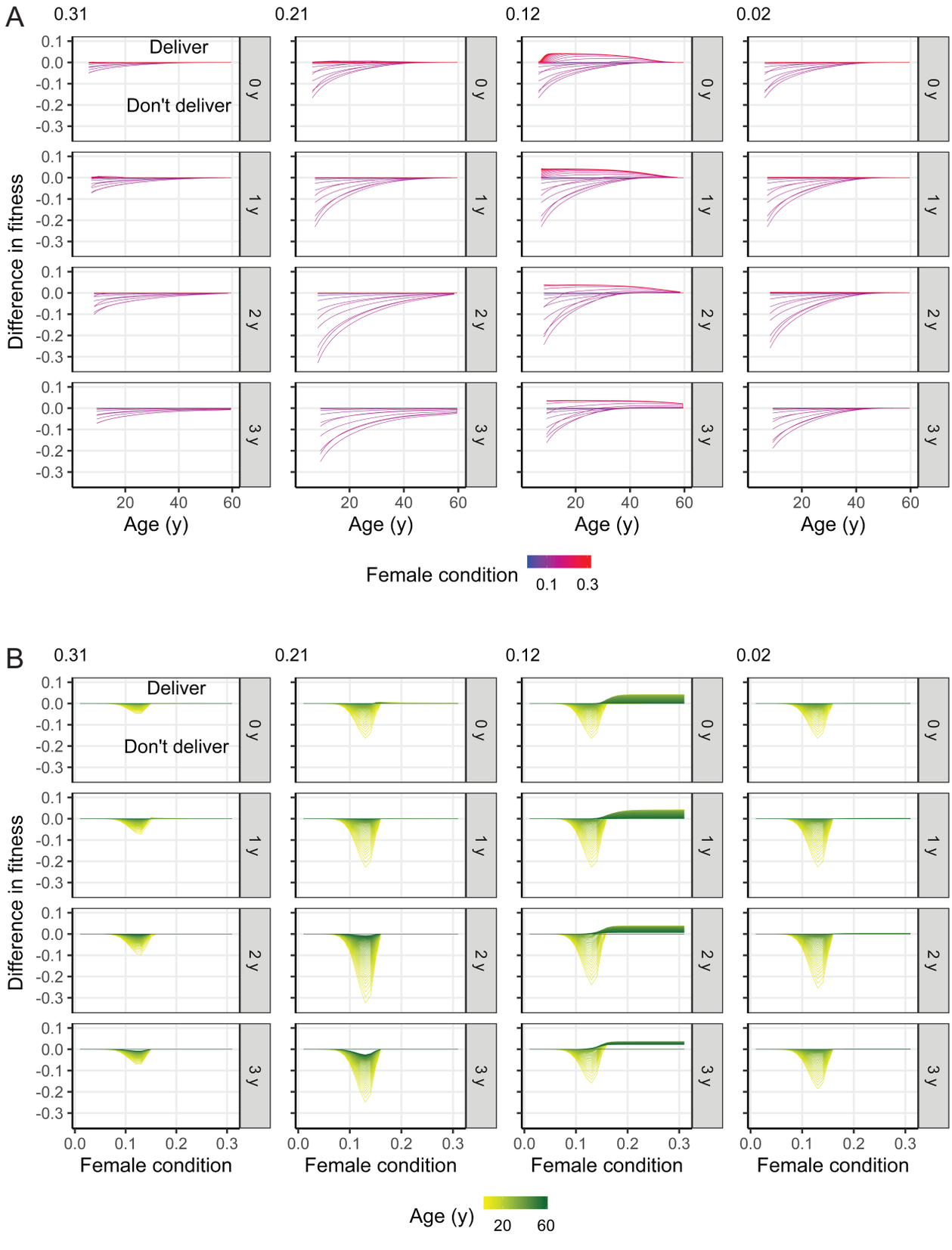

Figure 4: Difference in fitness value in model V1 between the decision to deliver milk and the decision to not deliver milk, highlighting the costs or benefits of lactation as a function of female age by female condition (*A*) and as a function of female condition by female age (*B*), given the dependent calf's age (rows; newborn, 1, 2, or 3 years) and condition (columns; 0.31, 0.21, 0.12, or 0.02).

in reproduction until later in life, when females were larger and thus had larger absolute reserves (e.g., fig. E9).

Disturbance Scenarios

Mean life-history statistics were strongly affected by disturbance (table E1; figs. 5, 6), and overall, the effects of disturbance on fitness were larger than those predicted by the DEB model (Hin et al. 2019). Under most disturbance scenarios, lifetime reproductive output collapsed, with most calves not surviving to weaning and the interbirth interval decreasing as the female attempted to initiate new reproductive cycles. Postweaning life expectancy was also reduced, although comparatively less than lifetime reproductive output and more so in more seasonal environments. In general, individuals attempted to reproduce early in life. While this strategy bore no cost in the absence of disturbance, it caused most of these young females to approach the starvation threshold and then die when feeding was impeded by disturbance. When the amplitude of seasonality was low ($A \leq 0.15$), females that survived through this initial bottleneck performed well for the remainder of their lives (e.g., fig. E10). The effects of disturbance were greater when females were disturbed in periods

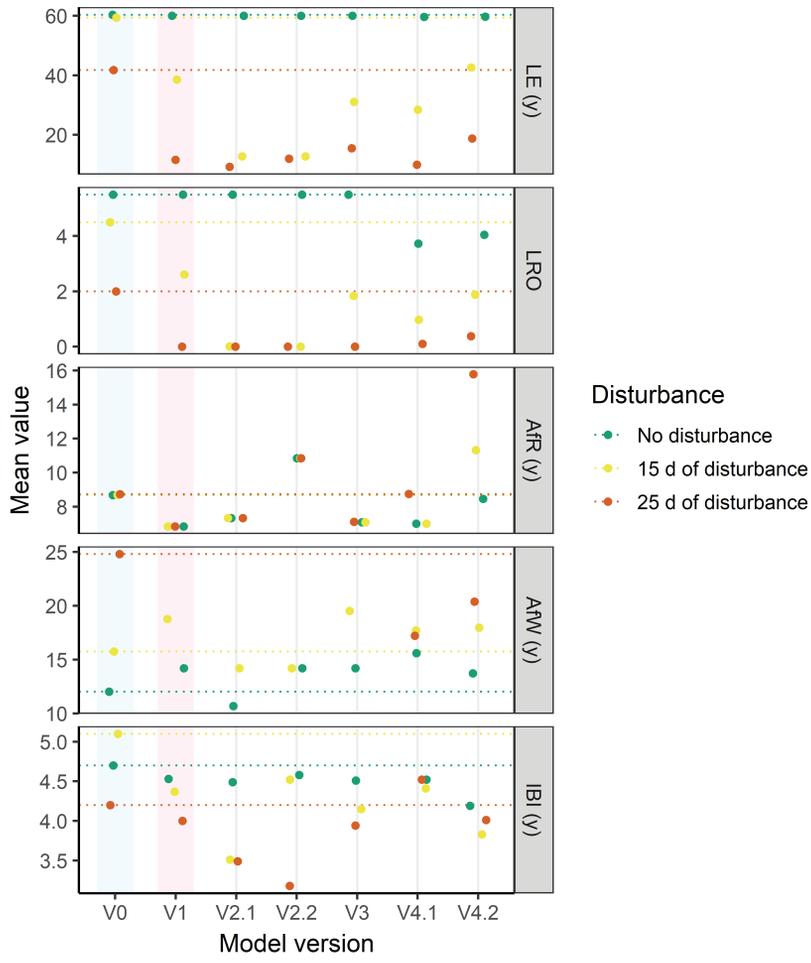

Figure 5: Mean life-history statistics emerging from all model versions under scenarios belonging to simulation set 1 ($\bar{R} = 1.8$, $A = 0$, disturbance duration = 0, 15, or 25 days). Life-history statistics are life expectancy (LE), lifetime reproductive output (LRO), age at first reproduction (AfR), age at first weaning (AfW), and interbirth interval (IBI). Model V0 indicates the original model by Hin et al. (2019), and results are shaded in blue. Results of the basic stochastic dynamic programming model V1 are shaded in red. In model V2, females could modulate milk delivery, without (V2.1) or with (V2.2) a constraint on age at first reproduction. In model V3, resource availability varied stochastically at a daily scale. In model V4, resource availability varied at a yearly scale and females did not (V4.1) or did (V4.2) have correct knowledge of such variation. Dotted lines indicate mean values from Hin et al. (2019). Females could die only of starvation-induced mortality.

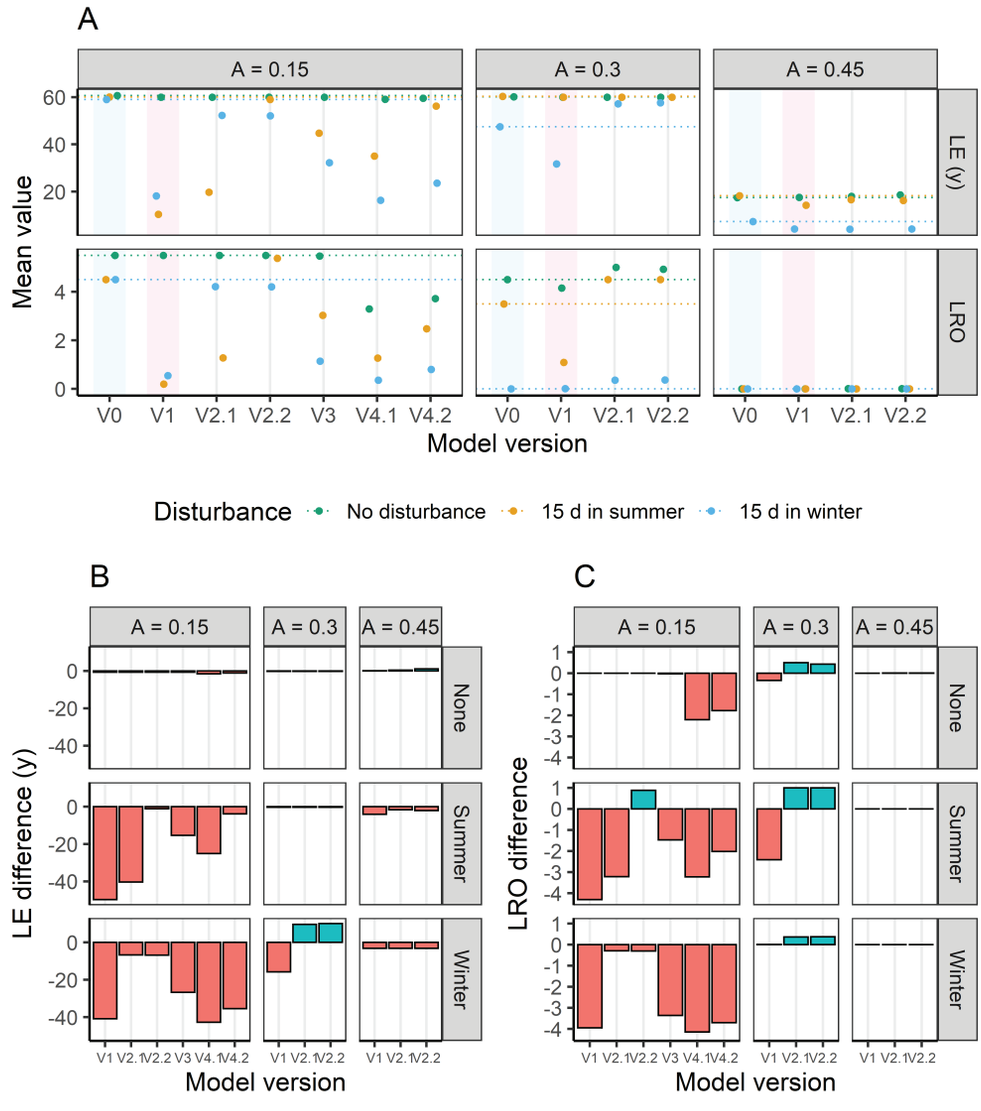

Figure 6: Life expectancy (LE) and lifetime reproductive output (LRO) emerging from all model versions under simulated scenarios belonging to simulation set 2 ($\bar{R} = 1.8$; $A = 0.15$, 0.3, or 0.45; disturbance duration = 0 or 15 days). Model V0 indicates the original model by Hin et al. (2019), and results are shaded in blue. Results of the basic stochastic dynamic programming model V1 are shaded in red. In model V2, females could modulate milk delivery, without (V2.1) or with (V2.2) a constraint on age at first reproduction. In model V3, resource availability varied stochastically at a daily scale. In model V4, resource availability varied at a yearly scale and females did not (V4.1) or did (V4.2) have correct knowledge of such variation. *A*, Mean values. Dotted lines indicate mean values from Hin et al. (2019). *B*, *C*, Changes in life expectancy (*B*) and changes in lifetime reproductive output (*C*) when each model version is compared with model V0; a red bar indicates a decrease in the corresponding life-history statistic, while a blue bar indicates an increase. "None," "Summer," and "Winter" indicate no disturbance, 15 days of disturbance in summer, and 15 days of disturbance in winter, respectively. Females could die only of starvation-induced mortality. Results for other life-history statistics are summarized in figure F8, available online.

of low resource availability (winter) than when resources were more abundant (summer; figs. 6, E3). There were some exceptions to this pattern; for example, high mortality was associated with the first reproductive attempt if this coincided with the occurrence of disturbance in summer (e.g., when $A = 0.15$).

Model Variants

Version V2: Graded Milk Delivery. When females could adjust milk delivery more finely, their strategy in a nonseasonal environment was riskier. They were able to follow the starvation threshold more closely and optimize energy

delivery to the calf, leading to earlier and more successful reproductive attempts (fig. F1). This also resulted in a different strategy regarding milk delivery (fig. F2), which continued for longer and brought the calf to a better condition at weaning, mimicking the results from the DEB model (Hin et al. 2019). In a nonseasonal environment, this riskier strategy resulted in an even greater sensitivity to disturbance than in model V1, with most females dying at the first reproductive attempt (table F1; fig. 5). However, in a seasonal environment, female resilience to disturbance improved compared with V1, possibly via a combination of lower risk-taking (because of the adaptation of reproductive strategy to oscillations in resources) and greater ability to adjust milk delivery based on body condition and resource availability (figs. 6, F3). With $A = 0.15$, life expectancy still suffered from the risks of early reproductive attempts when disturbance occurred in summer. However, when we forced females to wait until the age at which they first reproduced in the DEB model (Hin et al. 2019; 8.68 years; V2.2), they did not incur early mortality, leading to further improvements in life-history statistics in seasonal environments (table F1). For some combinations of conditions, V2.1 and V2.2 led to improved female resilience compared with the DEB model.

Version V3: Daily Resource Variation. In the absence of seasonality, the introduction of daily stochasticity in resource availability did not lead to an improvement in female ability to counteract the effects of disturbance compared with model V1 (table F1; figs. 5, F4). However, when paired with seasonality ($A = 0.15$; figs. 6, F5), there was a reduction of the effects of disturbance (in terms of both life expectancy and lifetime reproductive output), mostly via a higher chance of surviving through the first reproductive attempt.

Version V4: Yearly Resource Variation. In a nonseasonal environment ($A = 0$) that varied annually, mean life-history statistics did not improve, irrespective of the level of knowledge that the female was assumed to have (table F1; figs. 5, F6). Even in the absence of disturbance, yearly variation in resource availability led to a decline in lifetime reproductive output, while life expectancy could be maintained. In a seasonal environment ($A = 0.15$), life expectancy and lifetime reproductive output improved compared with model V1 but did not reach the values achieved in the DEB model (table F1; figs. 6, F7). As for $A = 0$, lifetime reproductive output suffered a decline in the absence of disturbance. Knowledge of the correct temporal scale of resource variation (model V4.2 vs. model V4.1) led to higher life expectancy and lifetime reproductive output.

Discussion

The reproductive strategy adopted by an individual emerges in response to complex, multidimensional problems that change dynamically over the course of its lifetime, particularly in long-lived species with large parental investment per reproductive event (Hirshfield and Tinkle 1975; Stearns 1992; Eberhardt 2002). Building on a DEB model for a long-lived whale species, we used SDLHT to show how reproductive decisions varied as a function of the age and condition of a female and her calf (McNamara and Houston 1996). In line with our results, a minimum length is required for sexual maturation in female pilot whales, and reproductive investments (e.g., the duration of lactation) vary over the course of life (Martin and Rothery 1993). The trade-off between the needs of the offspring and the mother (or parent-offspring conflict) also varied with stage of reproduction and resource availability (Trivers 1974), as observed in other marine mammal populations; for example, depending on the age of the offspring, polar bears (*Ursus maritimus*) differentially terminate or reduce investment in lactation when access to food is restricted (Derocher et al. 1993). In pinnipeds, while pregnancy rates in early gestation are high, abortion at later stages could be used as a mechanism to enhance performance during poor resource availability (Pitcher et al. 1998).

We then used the model to assess the sensitivity of model predictions to some of the assumptions surrounding this decision-making process. We showed that strategies finely tuned to predictable resource availability led to increased susceptibility to food limitation following disturbance, while more cautious strategies emerging under scenarios of unpredictable resource variation could improve resilience to novel conditions. Reproductive strategies derived from simpler, fixed rules were overall more robust to disturbance, without a loss of performance in stationary conditions. These results have important implications for both modeling and managing the consequences of anthropogenic disturbance on a population's dynamics.

Fixed Rules and Facultative Reproductive Behaviors

In the absence of anthropogenic disturbance causing an interruption of feeding activity, the reproductive strategy obtained from the maximization of lifetime fitness resulted in life-history statistics that were comparable to those associated with a strategy derived from fixed rules, designed to avoid starvation mortality (Hin et al. 2019). However, facultative reproductive behaviors influenced the way in which this outcome was achieved and caused a much lower resilience to disturbance compared with the DEB model.

Reproductive decisions were optimized in an environment with predictable, even if varying, resource availability.

As a result, females attempted to reproduce early in life and invested as much energy as possible in the first part of lactation, when the calf completely depended on milk. The reduced body condition that ensued meant that females and their calves were less able to cope with unexpected interruptions of feeding resulting from disturbance. Inability to predict how long disturbance events would last also meant that facultative reproductive behavior was not adjusted until it was too late and female condition was severely depleted, resulting in starvation-induced mortality. As a result, only one of the explored model variants (model V2) generated a higher lifetime reproductive output than predicted by the DEB model with fixed rules. The safer strategy derived from fixed rules could be interpreted in terms of bet hedging (Philippi and Seger 1989), ensuring a fitness advantage when individuals were confronted with new conditions, such as disturbance.

The relatively simple, fixed rules used in the DEB model were thus much more robust to novel conditions while not resulting in a loss in performance in stationary conditions. In contrast, complex, finely tuned strategies were predicted to fail when confronted with altered conditions. Because most animals live in environments where resource availability varies in space and time following multiscale autocorrelation patterns (Levin 1994), one important implication of our results is that such fragile strategies may be unlikely to evolve and persist in most systems, with the exception of contexts where resource dynamics are highly predictable and invariant over time. Similarly, Sultan and Spencer (2002) predicted that specialist strategies will prevail only if the costs of plasticity are large.

Propensity for Risk

Emerging differences in life-history strategy between the DEB model and the SDLHT model reflected the propensity of simulated females to take energetic risks. While the fixed rules in the DEB model resulted in females avoiding risks, the optimization of reproductive behavior via SDP could promote risk propensity. Propensity for risk is increasingly recognized as an important driver of life-history evolution (Wright et al. 2019). The results of our model variants revealed that under an optimized strategy the propensity to allow energy reserves to approach the starvation threshold, and the resulting susceptibility to disturbance, were affected by physiological constraints on energy investment toward reproduction (Zera and Harshman 2002) and by resource availability (Frank and Slatkin 1990). Generally, a lack of resource variation left individuals unprepared for situations where feeding was prevented by disturbance: individuals tailored their strategy on the expectation of food resources that could reliably support energy replenishment. In contrast, when the baseline condition included unpredictable variation in resource availability, females were regularly exposed to the risk of being unable to feed or of feeding less profitably. Even though resource heterogeneity made individuals more susceptible to disturbance during periods of low food availability, it also led to more resilient reproductive behaviors that accounted for unforeseen variation in the future (Schlichting and Pigliucci 1998; Snell-Rood 2013). These results support the idea that optimal phenotypes differ depending on whether resource availability is constant or fluctuating (Tuljapurkar et al. 2009). Imperfect knowledge about which decision is optimal could also steer individuals away from risky strategies (Johnson et al. 2013; see app. G). These predictions are supported by empirical evidence—for example, different levels of resource variation and knowledge thereof (as in models V3 and V4) have been shown to result in gradients of behavioral and reproductive plasticity in terrestrial mammals (Weaver et al. 1996) and birds (Dawson 2008). Moreover, birds adjust the amount of reserves they accumulate depending on the predictability of resources (Ekman and Hake 1990) and social ranking, which affects access to food (Ekman and Lilliendahl 1993). A wide geographical range exposes individuals to heterogeneous conditions and is therefore also expected to promote phenotypic plasticity, including in marine mammals (Pinsky et al. 2010).

The long-finned pilot whale population used to parameterize the model inhabits a seasonal environment, as reflected in seasonal variation in diet, body condition, and breeding (Desportes and Mouritsen 1993; Lockyer 1993; Martin and Rothery 1993). Interannual resource variability has also been associated with shifts in diet and distribution (Desportes and Mouritsen 1993; Hátún et al. 2009). Similarly, the congeneric species—short-finned pilot whales (*Globicephala macrorhynchus*)—shows some interpopulation life-history variation that has been linked to different levels of seasonality (Kasuya and Tai 1993). Under these heterogeneous resource conditions and over the large ranges occupied, it is therefore likely that pilot whales have evolved high plasticity and low propensity to risk with regard to reproductive decisions, possibly driven by simple rules as in the DEB model, which would make them comparatively more resilient to anthropogenic disturbance.

Critical Reproductive Decisions

Overall, risk propensity around the age at first reproduction and the timing and quantity of milk delivery had the largest influence on a female's resilience to perturbations. In nature, these decisions may be partly subject to

physiological constraints, which could protect the female from risky decisions. For example, a threshold age and size for sexual maturity would prevent her from attempting to reproduce when small size constrains the ability to accumulate sufficient reserves (e.g., Sand 1996). Long-finned pilot whales have to reach a minimum body size before they can engage in reproduction (Martin and Rothery 1993); because growth is fixed in our model, this constraint corresponds to setting a minimum age at first reproduction (as in model V2.2), which protects a female from the mortality associated with early reproductive attempts. With regard to lactation, other terrestrial (e.g., Chan-McLeod et al. 2009) and marine (Iverson et al. 1993; Crocker et al. 2001) mammals are known to flexibly adjust the quantity and energy content of milk delivered as a function of their nutritional status and the stage of lactation, a feature of lactation that increased female resilience in model V2.

Implications for the Management of Anthropogenic Stressors

The importance of physiological constraints and resource availability on risk propensity has implications for the susceptibility of individual vital rates to disturbance and the management of human activities that can cause such disturbance (Canale and Henry 2010). Our results suggest that individuals living in environments where there is limited spatial and temporal heterogeneity in resource availability could be particularly susceptible to perturbations, because their physiology and life-history strategy are adapted to a predictable status quo and may be inflexible to variation (Meyers and Bull 2002; Hendry 2016). Their risk propensity could rapidly become maladaptive if resource availability underwent sudden changes. In contrast, individuals living in more variable conditions are likely to exhibit plastic decision-making and risk awareness that allow an adjustment to unprecedented changes (e.g., Weaver et al. 1996; Dawson 2008). Our study highlights that baseline variation in resource availability has a critical influence on the ability to cope with disturbance (Canale and Henry 2010) and should therefore be quantified in future empirical work. This has repercussions for the management of anthropogenic stressors in the context of climate change: unpredictable changes or extreme events could lead to maladaptive responses if the correlation between proximate cues and fitness is disrupted—that is, if these cues become unreliable indicators of optimality (Reed et al. 2010). For example, the migratory behavior of blue whales (*Balaenoptera musculus*) is driven by historical mean resource availability rather than contemporaneous conditions (exemplifying the comparison between models V4.1 and V4.2), but this could make it hard for the species to adjust to rapid environmental changes (Abrahms et al. 2019). In contrast, individual variation in foraging strategy and propensity for risk among northern elephant seals (*Mirounga angustirostris*), evolved under periodic climatic oscillations, could modulate the adaptive ability of the species (Abrahms et al. 2018).

Our results also have important methodological implications: SDLHT models were highly sensitive to assumptions about the patterns of resource availability in the environment. Accurate predictions of the population consequences of disturbance using this approach will thus depend on the appropriate characterization of the spatial and temporal variability of food resources, and using simple reproductive rules might be more effective in many contexts. However, investigating optimal reproductive strategies will remain important in populations that inhabit environments where resource dynamics are highly predictable and finely tuned strategies could thus result in greater susceptibility to disturbance (Weaver et al. 1996; Dawson 2008; Canale and Henry 2010).

Conclusions

Bioenergetic models are emerging as an important tool to predict the population-level consequences of disturbance from human activities that can cause changes in the behavior and physiology of exposed individuals (Farmer et al. 2018; McHuron et al. 2018; Pirotta et al. 2018*a*, 2018*b*, 2019; Hin et al. 2019). Our study showed that, in the absence of disturbance, facultative reproductive behavior resulted in fitness comparable to the DEB model, while in all but one disturbed scenario fixed rules ensured a higher resilience to impaired feeding activity. Analysis of the way in which individuals may optimize their reproductive strategies in the light of internal and external state variables via SDLHT could help refine future developments of the fixed rules used in DEB models. For example, the energetic thresholds prompting various reproductive decisions could be made a function of the age of a female. More generally, these methods allow the multiple factors that affect an individual's decisions to be explored (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). Populations where individual reproductive strategy is adapted to optimize fitness are likely to be vulnerable to the effects of disturbance, particularly if that strategy evolved under highly predictable resource availability. The need to simulate scenarios of increasing fidelity for management will likely involve accounting for conflicting drivers of reproductive behavior, and the dynamic trade-offs that are required as internal physiology and external resource availability vary. Our study demonstrates that capturing this complexity is critical when predicting the population consequences of disturbance and that different assumptions

about the animals' risk propensity and ability to compensate for an unbalanced energy budget can drastically affect the conclusions drawn from any modeling effort.

Acknowledgments

E.P., V.H., J.H., L.N., and D.P.C. were supported by Office of Naval Research (ONR) grant N00014-16-1-2858 ("PCoD+: Developing Widely-Applicable Models of the Population Consequences of Disturbance"). D.P.C. was supported by the Exploration and Production Sound and Marine Life Joint Industry Project of the International Association of Oil and Gas Producers. A.M.d.R. and V.H. were funded by European Research Council Grant no. 322814 awarded to A.M.d.R. M.M. was supported by ONR grant N00014-19-2494. We thank Elizabeth McHuron, Lisa Schwarz, Cormac Booth, and Len Thomas for useful discussions during the development of this work. Thanks to Emer Rogan and University College Cork for providing desk space to E.P. The manuscript greatly benefited from the input and comments of editors Jennifer Lau and Jürgen Groeneveld and two anonymous reviewers.

Statement of Authorship

All authors contributed to conceiving the original idea. E.P. developed the model, building on the model developed by A.M.d.R., J.H., and V.H. V.H., M.M., J.H., and L.N. provided guidance to E.P. during model development. E.P. coded the simulations and analyzed the results. All authors participated in the interpretation of the results. E.P. led the writing of the manuscript. All authors contributed critically to the drafts and revisions of the manuscript.

Literature Cited

Abrahms, B., E. L. Hazen, E. O. Aikens, M. S. Savoca, J. A. Goldbogen, and S. J. Bograd. 2019. Memory and resource tracking drive blue whale migrations. Proceedings of the National Academy of Sciences of the USA 116:5582–5587.

Abrahms, B., E. L. Hazen, S. J. Bograd, J. S. Brashares, P. W. Robinson, K. L. Scales, D. E. Crocker, et al. 2018. Climate mediates the success of migration strategies in a marine predator. Ecology Letters 21:63–67.

Canale, C. I., and P. Y. Henry. 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Climate Research 43:135–147.

Chan-McLeod, A. C. A., R. G. White, and D. F. Holleman. 2009. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Canadian Journal of Zoology 72:938–947.

Clark, C. W., and M. Mangel. 2000. Dynamic state variable models in ecology. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford.

Costa, D. 2012. A bioenergetics approach to understanding the population consequences of acoustic disturbance. Pages 423–426 *in* A. N. Popper and A. Hawkins, eds. The effects of noise on aquatic life. Springer, New York.

Crocker, D. E., J. D. Williams, D. P. Costa, and B. J. Le Boeuf. 2001. Maternal traits and reproductive effort. Ecology 82:3541–3555.

Dall, S. R. X., and R. A. Johnstone. 2002. Managing uncertainty: information and insurance under the risk of starvation. Philosophical Transactions of the Royal Society B 357:1519–1526.

Dawson, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Philosophical Transactions of the Royal Society B 363:1621–1633.

Derocher, A. E., D. Andriashek, and J. P. Y. Arnould. 1993. Aspects of milk composition and lactation in polar bears. Canadian Journal of Zoology 71:561–567.

de Roos, A. M., N. Galic, and H. Heesterbeek. 2009. How resource competition shapes individual life history for nonplastic growth: ungulates in seasonal food environments. Ecology 90:945–960.

Desportes, G., and R. Mouritsen. 1993. Preliminary results on the diet of long-finned pilot whales off the Faroe Islands. Report of the International Whaling Commission 14:305–324.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Eddelbuettel, D., and R. Francois. 2011. Rcpp: seamless R and C++ integration. Journal of Statistical Software 40:1–18.

Ekman, J. B., and M. K. Hake. 1990. Monitoring starvation risk: adjustments of body reserves in greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. Behavioral Ecology 1:62–67.

Ekman, J. B., and K. Lilliendahl. 1993. Using priority to food access: fattening strategies in dominance-structured willow tit (*Parus montanus*) flocks. Behavioral Ecology 4:232–238.

Farmer, N. A., K. Baker, D. G. Zeddies, S. L. Denes, D. P. Noren, L. P. Garrison, A. Machernis, et al. 2018. Population consequences of disturbance by offshore oil and gas activity for endangered sperm whales (*Physeter macrocephalus*). Biological Conservation 227:189–204.

Frank, S. A., and M. Slatkin. 1990. Evolution in a variable environment. American Naturalist 136:244–260.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265–268.

Hátún, H., M. R. Payne, G. Beaugrand, P. C. Reid, A. B. Sandø, H. Drange, B. Hansen, et al. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. Progress in Oceanography 80:149–162.

Hendry, A. P. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. Journal of Heredity 107:25–41.

Hin, V., J. Harwood, and A. M. de Roos. 2019. Bio-energetic modeling of medium-sized cetaceans shows high sensitivity to disturbance in seasons of low resource supply. Ecological Applications 29:e01903.

Hirshfield, M. F., and D. W. Tinkle. 1975. Natural selection and the evolution of reproductive effort. Proceedings of the National Academy of Sciences of the USA 72:2227–2231.

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behavior: an approach based on state. Cambridge University Press, Cambridge.

Iverson, S. J., W. D. Bowen, D. J. Boness, and O. T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). Physiological Zoology 66:61–88.

Johnson, D. D. P., D. T. Blumstein, J. H. Fowler, and M. G. Haselton. 2013. The evolution of error: error management, cognitive constraints, and adaptive decision-making biases. Trends in Ecology and Evolution 28:474–481.

Kasuya, T., and S. Tai. 1993. Life history of short-finned pilot whale stocks off Japan and a description of the fishery. Report of the International Whaling Commission 14:439–474.

Kooijman, S. A. L. M. 2009. Dynamic energy budget theory for metabolic organisation. 3rd ed. Cambridge University Press, Cambridge.

Levin, S. A. 1994. Patchiness in marine and terrestrial systems: from individuals to populations. Philosophical Transactions of the Royal Society B 343:99–103.

Lockyer, C. H. 1993. Seasonal changes in body fat condition of northeast Atlantic pilot whales, and their biological significance. Report of the International Whaling Commission 14:325–350.

Mangel, M., and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, NJ.

Martin, A. R., and P. Rothery. 1993. Reproductive parameters of female long-finned pilot whales (*Globicephala melas*) around the Faroe Islands. Report of the International Whaling Commission 14:263–304.

McHuron, E. A., D. P. Costa, L. Schwarz, and M. Mangel. 2017. State-dependent behavioural theory for assessing the fitness consequences of anthropogenic disturbance on capital and income breeders. Methods in Ecology and Evolution 8:552–560.

McHuron, E. A., L. K. Schwarz, D. P. Costa, and M. Mangel. 2018. A state-dependent model for assessing the population consequences of disturbance on income-breeding mammals. Ecological Modelling 385:133–144.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature 380:215–221.

Meyers, L. A., and J. J. Bull. 2002. Fighting change with change: adaptive variation in an uncertain world. Trends in Ecology and Evolution 17:551–557.

National Academies. 2017. Approaches to understanding the cumulative effects of stressors on marine mammals. National Academies Press, Washington, DC.

Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution 4:2–5.

Pinsky, M. L., S. D. Newsome, B. R. Dickerson, Y. Fang, M. Van Tuinen, D. J. Kennett, R. R. Ream, et al. 2010. Dispersal provided resilience to range collapse in a marine mammal: insights from the past to inform conservation biology. Molecular Ecology 19:2418–2429.

Pirotta, E., C. G. Booth, D. P. Costa, E. Fleishman, S. D. Kraus, D. Lusseau, D. Moretti, et al. 2018*a*. Understanding the population consequences of disturbance. Ecology and Evolution 8:9934–9946.

Pirotta, E., V. Hin, M. Mangel, L. New, D. P. Costa, A. M. de Roos, J. Harwood. 2020. Data from: Propensity for risk in reproductive strategy affects susceptibility to anthropogenic disturbance. American Naturalist, Open Science Framework Repository, https://doi.org/10.17605/OSF.IO/G8DQ2.

Pirotta, E., M. Mangel, D. P. Costa, J. Goldbogen, J. Harwood, V. Hin, L. M. Irvine, et al. 2019. Anthropogenic disturbance in a changing environment: modelling lifetime reproductive success to predict the consequences of multiple stressors on a migratory population. Oikos 128:1340–1357.

Pirotta, E., M. Mangel, D. P. Costa, B. Mate, J. Goldbogen, D. M. Palacios, L. Huckstadt, et al. 2018*b*. A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. American Naturalist 191:E40–E56.

Pitcher, K., D. Calkins, and G. Pendleton. 1998. Reproductive performance of female Steller sea lions: an energetics-based reproductive strategy? Canadian Journal of Zoology 76:2075–2083.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Reed, T. E., S. W. Robin, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. Proceedings of the Royal Society B 277:3391–3400.

Roff, D. 1993. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. Oecologia 106:212–220.

Schlichting, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, MA.

Sibly, R. M., V. Grimm, B. T. Martin, A. S. A. Johnston, K. Kulakowska, C. J. Topping, P. Calow, et al. 2013. Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods in Ecology and Evolution 4:151–161.

Snell-Rood, E. C. 2013. An overview of the evolutionary causes and consequences of behavioural plasticity. Animal Behaviour 85:1004–1011.

Stark, J. D., J. E. Banks, and S. Acheampong. 2004. Estimating susceptibility of biological control agents to pesticides: influence of life history strategies and population structure. Biological Control 29:392–398.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

Sultan, S., and H. Spencer. 2002. Metapopulation structure favors plasticity over local adaptation. American Naturalist 160:271–283.

Trivers, R. 1974. Parent-offspring conflict. American Zoologist 14:249–264.

Tuljapurkar, S., J. M. Gaillard, and T. Coulson. 2009. From stochastic environments to life histories and back. Philosophical Transactions of the Royal Society B 364:1499–1509.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10:964–976.

Wright, J., G. H. Bolstad, Y. G. Araya-Ajoy, and N. J. Dingemanse. 2019. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. Biological Reviews 94:230–247.

Zera, A. J., and L. G. Harshman. 2002. The physiology of life history trade-offs in animals. Annual Review of Ecology and Systematics 32:95–126.

Associate Editor: Jürgen Groeneveld
Editor: Jennifer A. Lau